Taxonomic and functional biogeography of soil bacteria: importance of environmental filtering and dispersal depends on scale

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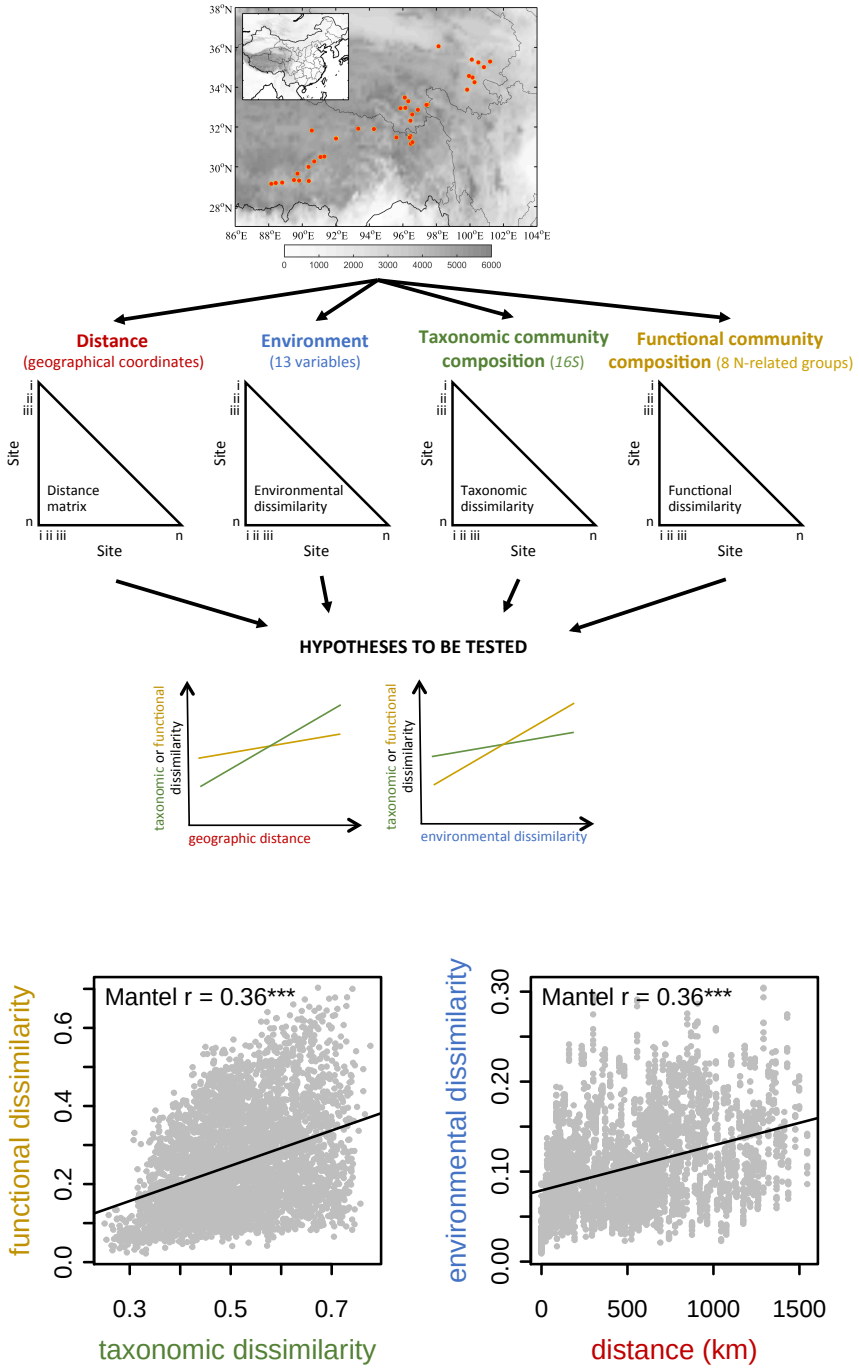
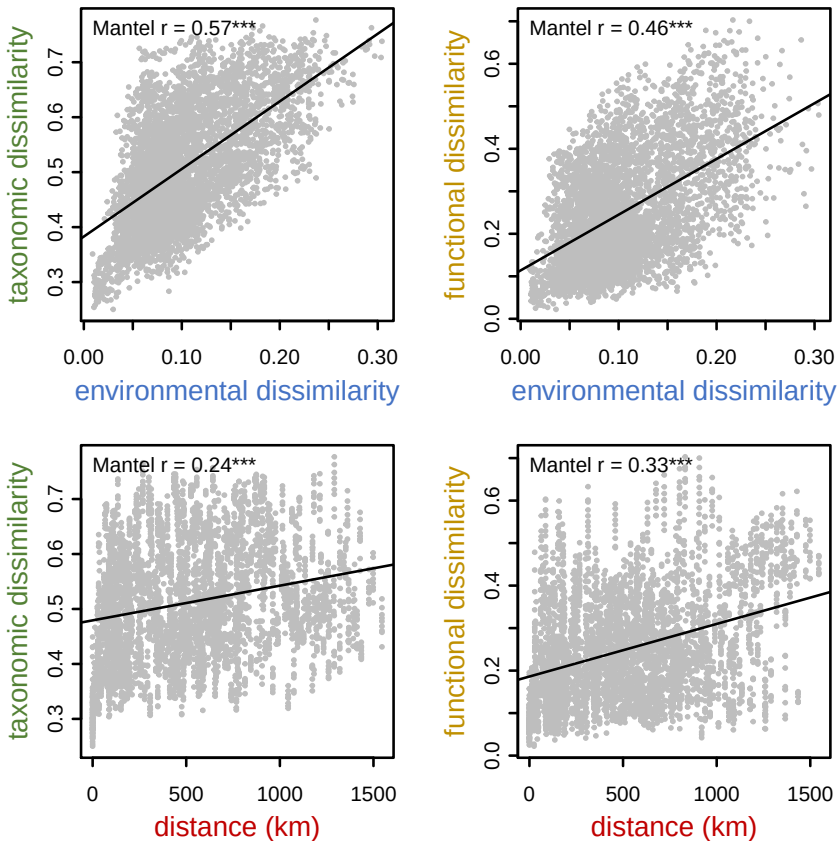
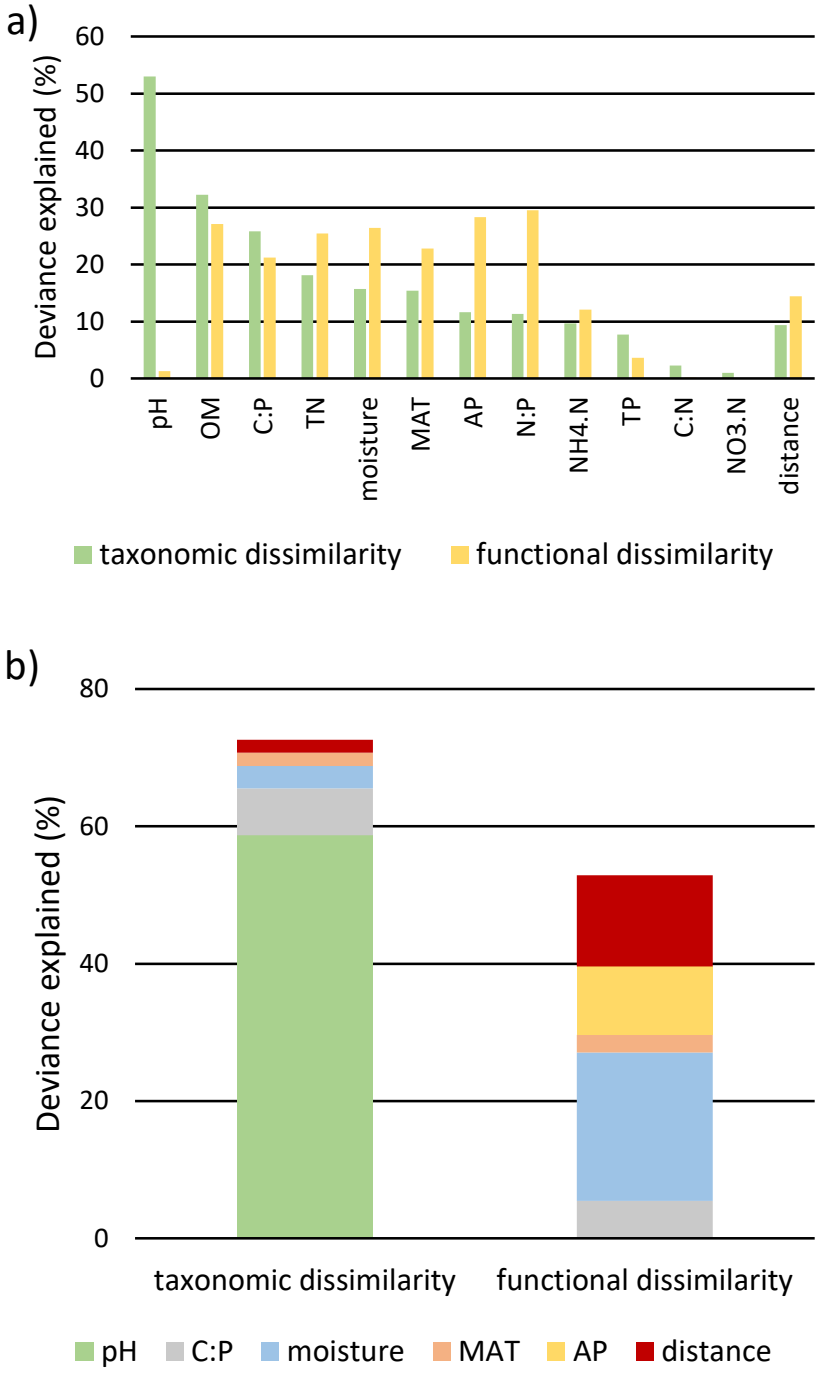
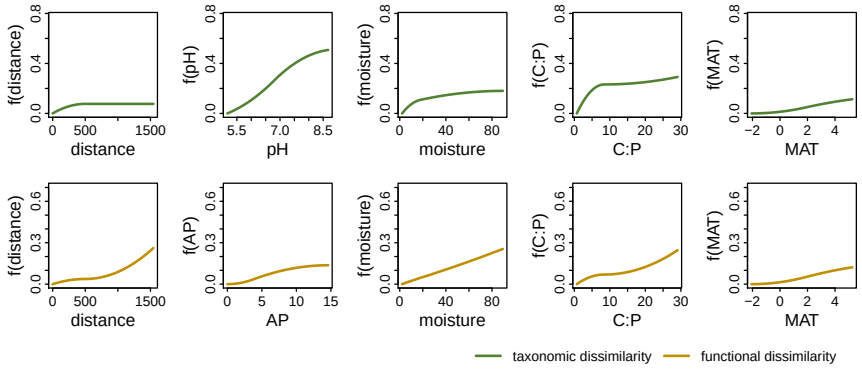
Abstract

The processes governing soil bacteria biogeography are still not fully understood. It remains unknown how the importance of environmental filtering and dispersal differs between bacterial taxonomic and functional biogeography, and whether their importance is scale-dependent. We sampled soils at 195 plots across the Tibet plateau, with distances among plots ranging from 20 m to 1,550 km. Taxonomic composition of bacterial community was characterized by 16S amplicon sequencing, and functional community composition by qPCR targeting 9 functional groups involved in N dynamics. Twelve climatic and soil characteristics were also measured. Both taxonomic and functional dissimilarities were more related to environmental dissimilarity than geographic distance. Taxonomic dissimilarity was mostly explained by soil pH and organic matter, while functional dissimilarity was mostly linked to moisture, temperature and N, P and C availabilities. The roles of environmental filtering and dispersal were, however, scale-dependent and varied between taxonomic and functional dissimilarities, with distance affecting taxonomic dissimilarity over short distances (<˜300 km) and functional dissimilarity over long distances (>˜600 km). The importance of different environmental predictors varied across scales more for functional than taxonomic dissimilarity. Our results demonstrate how biodiversity dimension (taxonomic versus functional) and spatial scale strongly influence the conclusions derived of bacterial biogeography.









Taxonomic and functional biogeography of soil bacteria: importance of environmental filtering and dispersal depends on scale

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Abstract

The processes governing soil bacteria biogeography are still not fully understood. It remains unknown how the importance of environmental filtering and dispersal differs between bacterial taxonomic and functional biogeography, and whether their importance is scale-dependent. We sampled soils at 195 plots across the Tibet plateau, with distances among plots ranging from 20 m to 1,550 km. Taxonomic composition of bacterial community was characterized by *16S* amplicon sequencing, and functional community composition by qPCR targeting 9 functional groups involved in N dynamics. Twelve climatic and soil characteristics were also measured. Both taxonomic and functional dissimilarities were more related to environmental dissimilarity than geographic distance. Taxonomic dissimilarity was mostly explained by soil pH and organic matter, while functional dissimilarity was mostly linked to moisture, temperature and N, P and C availabilities. The roles of environmental filtering and dispersal were, however, scale-dependent and varied between taxonomic and functional dissimilarities, with distance affecting taxonomic dissimilarity over short distances (<~300 km) and functional dissimilarity over long distances (>~600 km). The importance of different environmental predictors varied across scales more for functional than taxonomic dissimilarity. Our results demonstrate how biodiversity dimension (taxonomic versus functional) and spatial scale strongly influence the conclusions derived of bacterial biogeography.

Significance Statement

Our study demonstrates that i) in general, the importance of environmental filtering exceeds that of dispersal for both taxonomic and functional biogeography of soil bacteria; ii) taxonomic and functional biogeographic patterns are driven partly by different environmental drivers, with pH being the most important for taxonomic composition, while several variables drive the N-related functional composition; and iii) the importance of environmental filtering and geographic dispersal are scale-dependent, with dispersal being related to taxonomic dissimilarity at short distances only, but to functional dissimilarity only when distances are > 600 km. Overall, these findings show that taxonomic and functional components of soil bacterial communities are not constrained by the same drivers, and that interpretation of bacterial biogeography depends on the spatial scale.

Introduction

The composition of biological communities varies across space, expressed as gradually changing beta-diversity along geographical and environmental gradients, with a tendency to have distinct biological assemblages in different parts and habitats of a landscape (1-3). The knowledge of such patterns and their drivers regarding microorganisms, however, is scarce when compared to the knowledge available for macroscopic species (4-11). The famous hypothesis ‘everything is everywhere, but environment selects’ made by Baas Becking (12) suggests that the distribution of free-living microorganisms would be mainly governed by environmental selection (13). However, many recent studies have found that soil bacteria can show spatial patterns related to geographic isolation (14-17). Due to their passive dispersal regimes, soil bacteria might indeed be more dispersal-constrained than macroscopic and aquatic organisms (18-20). Overall, an increased understanding of the drivers of the distribution of soil microorganisms and of their community composition is still needed. This need is further

intensified in the context of ongoing global changes, such as climate warming, N deposition and acidification which affect biota distribution and assemblages (21, 22).

Following Vellend (23), Hanson, Fuhrman, Horner-Devine and Martiny (8) and Nemergut*, et al.* (24) distinguished four fundamental assembly processes defining the spatial patterns in diversity and composition of microbial communities: selection (through environmental filtering and biotic interactions), dispersal, drift and mutation/diversification, the main processes identified being environmental filtering and dispersal (7, 17, 25-31). Environmental filtering represents a process where environmental conditions shape community composition by filtering taxa that have suitable strategies to establish in a site. Dispersal affects community composition by influencing the establishment of organisms in new sites. Taken together, both processes lead to a distance decay effect where communities further away are less similar than the communities close-by, because of increasingly different environmental conditions and/or higher isolation with increasing distance (32-36). While dissimilarity of environmental conditions can correlate with geographical distance, environmentally similar conditions can be found from distant locations too, or reversely, sharp environmental transitions can occur across small distances (37). Thus, sampling soil bacterial communities over broad spatial and environmental transects including both fine- and broad-scale variations can allow tearing the effects of these two processes apart based on the covariance between bacterial community dissimilarity and environmental dissimilarity and geographic distance (38).

For soil bacteria, most studies on the relative roles of environmental filtering and dispersal have focused on community dissimilarity based on the taxonomic compositions of communities (14, 30, 39). However, bacterial communities can be assessed using other entities too, such as functional attributes, that do not necessarily correlate with taxonomy (40-43) because functional redundancy can be particularly high within bacterial communities (44). For example, communities in two distant but environmentally similar places might considerably differ taxonomically due to the dispersal barrier, whereas their functional composition might be relatively more similar due to prevailing environmental conditions favouring or requiring certain functions or functional attributes (40). Thus, the importance of environmental filtering and dispersal as drivers of soil bacteria biogeography might vary depending on the type of measure of communities used (45-47). More particularly, dispersal processes (and so geographic distance) would better explain taxonomic dissimilarity among soil bacterial communities, whereas some previous reports suggested that community functional dissimilarity, which is affected by local gradients in resource availability, might be less related to distance and more to environmental conditions (48) (Fig. 1). Incorporating both taxonomic and functional compositions of communities might better reveal the major drivers of soil bacterial biogeography (43, 49, 50). Since soil bacteria communities are connected to ecosystem functioning such as nutrient and carbon cycles (51-53), understanding bacterial biogeography from both the taxonomic and functional points of view is crucial to forecasting future impacts of global changes on ecosystems.

In this study we aim to advance the understanding of soil bacteria biogeography by analysing a large range of environments and distances, and incorporating both taxonomic and functional dissimilarities of bacterial communities, in order to compare the relative roles of environmental filtering and dispersal in explaining the taxonomic and functional biogeography of soil bacteria. For this purpose, we sampled soils along a 1,550 km transect across the Tibet

plateau (Fig. 1). Taxonomic community composition was defined based on the relative abundances of OTUs determined by *16S* amplicon sequencing, while one aspect of functional community composition was defined based on the abundances of nine nitrogen (N) cycle-related functional groups determined by quantitative PCR. For each plot, environmental conditions were derived based on 12 climatic and soil characteristics. The relationships between taxonomic, functional and environmental dissimilarities and geographic distances among sampling locations (calculated from geographic coordinates) were then assessed using mantel tests and general dissimilarity modelling (GDM; Fig. 1). We assumed that the taxonomic and functional community compositions would not be akin and that environmental dissimilarity and geographic distance would not correlate strongly. We also assumed that functional dissimilarity would better correlate with environmental dissimilarity than geographic distance (Fig. 1), with distinct predictors explaining taxonomic and functional compositions. We also evaluated the possible influence of spatial scale on the conclusions derived.

Results

When rarefying sequences to obtain 14,619 sequences for each of the 96 plots, a total of 6,384 different OTUs were observed across all the plots. The OTU richness varied from 1,371 to 2,164 OTUs per plot.

For the nine N-related functions, the largest variations in abundances among all plots were observed for the free N_2 fixers (*nifH*) and the *nosZ1*-N_2O reducers, with abundances ranging from 3.9×10^4 to 1.3×10^{10} and from 1.4×10^5 to 4.2×10^9 gene copies g^{-1} soil, respectively (Fig. S5). In comparison, *Nitrospira* abundance varied over three orders of magnitude. The less abundant groups were ammonia oxidizing AOB and the nitrite-oxidizing *Nitrobacter*, with median abundances across the 195 sites being 3.49 10^5 and 1.25 10^4 gene copies g^{-1} soil, respectively (Fig. S5).

Concerning the environmental variables, soil pH ranged from 5.17 to 9.08 for the 195 samples (Fig. S6). Soil organic matter concentration (OM) ranged from 0.3 % (for Alpine semi-desert shrub steppe) to 41.9 % (swamp meadow), though most values were below 20 %. Large variations were also observed for soil mineral N concentrations, i.e. from 0.95 to 52.25 ppm and 1 to 89.4 ppm for ammonium (NH4.N) and nitrate (NO3.N), respectively (Fig. S6). Mean annual temperature (MAT) varied from -3°C to 7°C. Some of the environmental variables were correlated, which included OM with total nitrogen concentration (TN) and with the soil C:P stoichiometric ratio; and TN with the soil N:P stoichiometric ratio (Table S2).

Relationships among taxonomic, functional and environmental dissimilarities and distance

Mantel tests performed on the 96 soil samples for which both taxonomic and functional compositions were available showed a positive correlation (r=0.36) between taxonomic and functional dissimilarities (Fig. 2). Environmental dissimilarity and distance had similarly positive correlation (r=0.36; Fig. 2). Both taxonomic and functional dissimilarities were positively correlated to environmental dissimilarity (r=0.56 and r=0.46, respectively) and less strongly to distance (r=0.24 and r=0.33; Fig. 3). Similar patterns were observed when using data from all 195 plots, where functional dissimilarity more strongly correlated with environmental dissimilarity than distance (r=0.50 and 0.31, respectively) (Fig. S7).

Predictors of taxonomic and functional dissimilarities

The environmental predictors reaching the highest explanatory power for taxonomic dissimilarity, when considered individually in GDMs, were soil pH (more than 50% of the variance explained) and to a lesser extent OM and C:P (32% and 26% of the deviance explained, respectively; Fig. 4a). For the functional dissimilarity, the N:P and available phosphorus had the highest explanatory power (nearly 30% of the deviance explained for each) followed by soil moisture, OM and TN (ca. 25% of the deviance explained for each; Fig. 4a). Distance explained 10-13 % of deviance of taxonomic and functional dissimilarity.

The best GDM for taxonomic dissimilarity explained 72% of the variance and included five predictors (ranked according to their relative predictor contribution): pH > C:P (highly correlated with OM) > soil moisture > MAT > distance (Fig. 4b). The best model for functional dissimilarity (based on the same 96 samples) explained 53 % of the variance and included 5 predictors (ranked according to their relative predictor contribution): soil moisture > distance > available phosphorus (AP) > C:P > MAT (Fig. 4b). Note that the C:P was highly correlated to the N:P and OM (Table S2). Similar results were obtained when the analysis was performed for all the 195 soil samples (Fig. S8).

Predictors' relationships to taxonomic and functional dissimilarity

The I-splines (response curves) fitted to the predictors retained in the best models showed that taxonomic dissimilarity was in continuous manner and strongly related to change in soil pH and with weaker amplitude to change in MAT among the plots (Fig. 5). In contrast, differences in soil moisture and C:P among the plots increased taxonomic dissimilarity the most strongly at lower ends of the gradients. Taxonomic dissimilarity increased with distance only when the plots were 20 m – 300 km apart.

Functional dissimilarity was related to differences in soil moisture, C:P and MAT among the plots in rather continuous manners along the observed gradients (Fig. 5). Difference in AP was mostly related to the functional dissimilarity at the lower end of the gradient. In contrast to the results obtained for taxonomic dissimilarity, the functional dissimilarity was mostly related to increase in distance when it was 600 km or more. These results were confirmed when analysing all the 195 soil samples (Fig. S9).

Scale dependency of processes driving bacterial biogeography

Correlations between taxonomic and functional dissimilarities and between environmental dissimilarity and distance were the strongest when the distances among plot pairs were 20 m – 314.3 km (r=0.55 and 0.33, respectively) than >314.3 km (r=0.16-0.24 and 0.05-0.07, respectively; Fig. S10 top). Correlations of taxonomic and functional dissimilarities to environmental dissimilarity were rather stable across the different distance classes (always between 0.47 and 0.64, except 0.23 between functional dissimilarity and environmental dissimilarity for medium distances; Fig. S10 middle row). Between taxonomic dissimilarity and distance, the significantly positive correlation (r=0.36) occurred when the distances among plot pairs were 20 m – 314.3 km (Fig. S10 bottom left). Between functional dissimilarity and distance, the correlation was strongest (r=0.32) when distances were 671 – 1,546 km (Fig S10 bottom right).

The GDMs showed that the importances of individual environmental predictors for

taxonomic dissimilarity were largely stable across the three scales (Fig 6a). In contrast, for functional dissimilarity the explanatory power of environmental predictors, especially of soil moisture, MAT, AP and NH4.N varied across the scales (Fig. 6b). Irrespective of the scale, soil pH, C:P, soil moisture and MAT were always included in the best model of taxonomic dissimilarity, with pH always having by far the largest relative predictor contribution (Fig. 6c). The predictors and their relative contributions in the best models for functional dissimilarity showed that soil moisture and C:P had a prominent role at the short scale but their relative importance decreased with increasing distance (Fig. 6c), where NH4.N, total phosphorus (TP) and distance became significant.

For the pairs of plots 20 m – 314 km apart, distance alone explained 24 % of deviance in taxonomic dissimilarity vs. 11 % in functional dissimilarity, whereas for the pairs of plots 671 – 1,546 km apart, these values were 0 % and 11 %, respectively. Distance was included as a predictor in the best model only at the short scale for taxonomic dissimilarity and at the long scale for functional dissimilarity.

Discussion

A good understanding of soil bacteria biogeography and its determinants is needed to better understand ecosystems' structures and functioning, and to anticipate their possible changes with global change (22, 54, 55). Here, we studied if and how environmental filtering and dispersal affect the taxonomic and N-related functional compositions of soil bacteria communities, hypothesising that, due to functional redundancy, environmental filtering would more strongly drive functional than taxonomic composition whereas dispersal would be relatively more important for taxonomic than functional composition. We based these hypotheses on the underlying expectations that the taxonomic and functional community compositions would not be akin, and that environmental dissimilarity and geographic distances among sites would not strongly correlate, thus allowing to unravel the effects of environmental filtering and dispersal.

Some hypotheses were supported by our analyses. In particular, taxonomic and functional community compositions were not tightly correlated, and we found support for the presence of functional redundancy (i.e. taxonomic dissimilarity was in general higher than functional dissimilarity as observed also, e.g., for fish assemblages (56)). However, in contradiction with our hypotheses, environmental filtering played a major role in comparison to dispersal for both taxonomic and functional compositions. Moreover, we observed a strong scale-dependency in the drivers of bacteria biogeography and the role of distance, which varied between taxonomic and functional biogeography. Below we elaborate on these findings in more detail.

The taxonomic biogeography of soil bacteria is mostly driven by pH, while their N-related functional biogeography is determined by a range of environmental conditions

The strong positive correlation between taxonomic and environmental dissimilarities was mainly related to soil pH and to a lesser extent to soil organic matter (correlated to the C:P ratio). The strong influence of pH on soil bacterial communities has been reported for different parts of the world, including Great Britain (6), USA (5, 57), the Western Swiss Alps (30) and China (58, 59), with the only exception being the report by Plassart*, et al.* (60) indicating that soil

bacterial composition varied greatly across a pan-European transect but that less than 5% of this variation was explained by soil pH. The overall conception is, thus, that pH is the major driver of soil bacterial communities by acting as a selective force for many bacterial taxa (61). This could be due to direct effects of pH on soil bacteria (62) but also to non-direct effects because pH often correlates with a number of other biotic and abiotic variables such as soil carbon and nitrogen substrate availabilities (63), plant community diversity (64) and composition (65), and bioavailability of some pollutants (66).

Yet, interestingly, we did not find pH as an important driver of functional community dissimilarity, here assessed based on functional genes related to nitrogen dynamics. This was not expected because some bacterial groups studied, e.g. AOB and *Nitrobacter,* are sensitive to pH (61). However, this finding might be due to the fact that the effect of soil pH on some N-related groups is mostly indirect, acting for instance through altered N availability and changed plant diversity (67). Thus, N availability would be a more straightforward variable to predict functional dissimilarity here. In addition, a weaker sensitivity to pH – in terms of abundance – of other groups like denitrifiers (68, 69) could explain the minor role of pH when explaining functional dissimilarity. Functional dissimilarity was mainly explained by the availabilities of N, C and P (and associated stoichiometric ratios) along with moisture and mean annual temperature. These drivers are largely consistent with the ecology of the 9 N-related functional groups studied and partly also identified in the study by Nelson, Martiny and Martiny (43). In addition, in grassland soils from the Tibetan plateau fertilised with N, P or NP, AOB, *Nitrobacter* and *Nitrospira* were sensitive to N availability and organic matter concentration, N_2-fixers to the N:P ratio, *nirS*-nitrite reducers to soil N and organic matter, and *nirK*-nitrite reducers to organic matter and the N:P ratio (70). Similarly, soil moisture often influences functional groups like nitrifiers and denitrifiers (71). Overall, the nature of the environmental drivers of functional dissimilarity obviously depends on the functional groups considered, and other environmental drivers would likely be important with a focus on other specific groups like degraders of specific molecules. The nine functional groups selected here, however, represent a consistent and rather comprehensive set of groups involved in major aspects of soil N dynamics, which is an important aspect of the functioning of ecosystems.

Our finding that environmental filtering does not happen through the same set of environmental variables for both taxonomic and functional dimensions is consistent with recent studies on Tibetan meadow soils reporting that the abundances of many bacterial functional groups involved in soil N dynamics depended on soil N availability, organic matter concentration and N:P ratio, but that the majority of bacterial taxa in the same soils were limited by other resources than N and P (70, 72). The same finding was done in global context by Nelson, Martiny and Martiny (43). Altogether, this has important implications to predict ecosystem functioning and anticipate the effect of global change (73). Especially, while soil acidification or alkalinisation would strongly change the taxonomic composition of bacterial communities, the functioning of bacterial communities would not necessarily respond to pH per se but rather to changes in C:N:P availability and soil moisture.

The importance of dispersal for taxonomic and functional community composition is weak and varies with scale

When considering all plots, distance was a weak predictor of functional and even more so of

taxonomic community composition. However, when performing our analyses at different spatial scales (i.e. distinguishing short, medium and long geographic distances among the pairs of plots), the role of distance varied between taxonomic and functional dissimilarity depending on the scale. In particular, the role of distance in explaining taxonomic dissimilarity was detected only at short scale (until a limit of ca. 300 km) after which the further distance had no further effect in taxonomic composition. Similarly, in the experiment of Lindström and Östman (74), dispersal affected taxonomic community composition only at high dispersal rates (which can be assumed to occur at shorter distances)and Shi*, et al.* (59) reported that stochastic processes (including dispersal) dominated over environmental filtering for the composition of soil bacterial communities when distances among study sites were short, whereas environmental filtering dominated over stochasticity for larger distances. A comparison of this scale-dependency against the results obtained for plant species would be important, since for them the effect of dispersal is commonly thought to act on coarser scale than environmental filtering (75, 76).

At coarser scales, i.e. when the plots are >651 km apart, distance became relatively more important in explaining functional dissimilarity. A strong role of distance was also observed at global scale in marine environments (49), where the authors hypothesised that the effect of distance on functional composition was due to historical evolutionary changes that select certain bacterial functions. This might also explain our finding, although the reasoning of Haggerty and Dinsdale (49) concern free-living communities.

Scale dependency of the environmental drivers of taxonomic and functional bacterial biogeography

Incorporating spatial scale to the analyses also modulated some conclusions regarding the importance of environmental predictors. While the dominant role of pH, and to some extent of OM, in explaining taxonomic dissimilarity did not vary across the scales, the main environmental predictors of functional dissimilarity did vary. A possible explanation for these results could be that the variation (i.e. heterogeneity; as measured by variances or ranges of values) of environmental variables changes among the scales (77). More specifically, a predictor that has less heterogeneity for a given distance class might not be identified as having an important role at this scale and vice versa. Indeed, there was some link between the variability (Fig. S11) and importance of the environmental predictors across the scales. For example, the variability of pH among the plots was relatively stable across the scales and so is its importance in explaining taxonomic dissimilarity, whereas variability of TP, NH4.N and MAT increased with distance between the plots, and these predictors also became significant and more important in explaining functional dissimilarity at coarser scales. Thus, it is important to bear in mind that the importance of an environmental driver might be linked to its variability across the study area when comparing the results of different studies covering different environmental heterogeneity. However, here, we did not observe any correlation across scales between the variance and importance of environmental variables for e.g. C:P, organic matter and AP, which suggests that the relative importance of drivers across scales could also be linked to modified environmental filtering processes. Analysing this in more detail would, however, require a different kind of setting.

Materials and methods

Study area and soil sampling

The study area covers a large part of the Tibetan Plateau and stretches 800 km along latitude and 1,250 km along longitude (Fig. 1). The climate is high altitude plateau climate with precipitation mainly falling during the short, cool summer in July and August (70). The mean annual temperature ranges from -15 to 5 °C (78) and mean annual precipitation from 170 to 600 mm (79). Soil sampling was performed randomly along a ca. 1,500 km SW-NE transect in the Qinghai Province and Tibetan Autonomous Region, China (Fig. 1), during the peak-growing season in July–August 2015. We collected soil samples from 39 sites. At each site, soil was sampled from five plots of 0.25 m^2 to 1 m^2 located at least 20 m from another (Fig. S1). From each plot, 5 soil cores (0–10 cm; 4 cm diameter) were collected and homogenized to form one composite sample per plot (i.e. 975 individual cores leading to 195 composite samples). The location and altitude of each site was measured using a Trimble JUNO SC GPS. The altitudes of the plots ranged from 2,988 m to 4,787 m above sea level.

Composite soil samples were sealed in plastic bags, stored a few days at 4 °C and brought back to the laboratory. Fresh sub-samples were used for measuring soil environmental variables. Other sub-samples were stored at -20°C for a few weeks before molecular biology assays. Extracted DNA was stored at -80℃ before sequencing and quantitative PCR assays (see below).

DNA extraction from soil and 16S rRNA sequencing

Total genomic DNA was extracted from samples using 0.25 g of soil, according to the MoBio Power Soil DNA isolation protocol (MO BIO laboratories, Carlsbad, CA, USA). The taxonomic compositions of bacterial communities were determined by amplifying the V4 hypervariable regions of bacterial 16S ribosomal RNA. This was done for 99 composite samples only, first by randomly selecting three plots from the five available at each of the 39 sites (39*3=117) and then removing 18 of these sites mostly redundant with other plots based on vegetation type. DNA was amplified using the 338F/806R primers (Table S1). Amplification problem was encountered for one site, finally leading to amplicons for 96 samples. Amplicons were extracted from 2 % agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The purified products were pooled in equimolar and paired-end sequenced on an Illumina MiSeq platform (Shanghai Majorbio Bio-pharm Technology Co., Ltd., Shanghai, China). Acquired sequences were quality-filtered using Trimmomatic (version 0.36). Singletons were removed before the OTU clustering step. Chimeras removing and operational taxonomic units (OTUs) clustering (3% dissimilarity cutoff) were performed with UPARSE (version 7.0.1090) (80). OTUs with less than two sequences were removed. Sequences were rarefied to obtain 14,619 sequences for each of the 96 plots. The raw sequence was submitted to NCBI Short Read Archive under accession number SRR11586107 - SRR11586107.

Quantitative PCR assays

Nine different functional groups involved in soil N cycling were targeted (Fig. S2). For all the 195 samples, the abundances of free N_2-fixers, ammonia oxidizing bacteria (AOB), two groups of nitrite oxidizing bacteria (*Nitrobacter* and *Nitrospira*), nitrate-reducers, two groups of nitrite-reducers, and two groups of N_2O-reducers were quantified by quantitative PCR targeting

sequences of the following genes (70): *nifH* (coding for the nitrogenase); bacterial *amoA* (coding for the bacterial ammonia monooxygenase); *nxrA* (coding for nitrite oxido-reductase specific of the bacterial genus *Nitrobacter*); *16S* specific of the bacterial genus *Nitrospira*; *narG* (coding the nitrate reductase); *nirK* and *nirS* (both coding for a nitrite reductase); and *nosZ*1 and *nosZ2* (coding for N_2O reductase), respectively. The abundances of *Nitrobacter* and *nosZ2*-N_2O reducers were quantified on a lightcycler 480 (Roche Dignostic, Meylan, France) using 20 ul reaction volume with 40 ng, and 25 ul with 20 ng of DNA templates, and 0.5 uM and 1 uM of each primer, respectively (see Table S1). The abundances of the seven other groups were quantified on an iCycler iQ5 thermocycler (Bio-Rad,USA), using 20 ml reaction volume with 2 µl of DNA templates, and 1.6 ml (0.8 mM) of each primer (Table S1) and 10 ml SYBR Premix ExTaq™II (Takara, Japan). Plasmids carrying sequences of the targeted genes were constructed by cloning the targeted gene fragments into plasmid pGEM-T Easy Vector (Promega, Madison, USA). Details of qPCR methodologies and standards used are presented in Table S1. Ten-fold serial dilutions of the linearized plasmid DNA were used to establish a standard curve for each gene, and the data were then transformed into gene copy numbers per gram of dry soil. Inhibition tests were performed on 64 samples (randomly chosen) for the *nifH* gene by diluting 5 and 10 times DNA extracts before qPCR, and this showed no inhibition.

Environment data measurement

For each of the 195 samples, eight soil characteristics plus one climatic factor were quantified. Soil organic matter concentration (OM) was determined by the potassium dichromate method (81). Total nitrogen (TN) and total phosphorus (TP) concentrations were determined with a SAN++ system flow injection analyzer (SAN++, Brampton, Canada) after digesting, according to Bao (2000). Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were measured using a SAN++ system flow injection analyzer after extraction with KCL (82). Available phosphorus (AP) was extracted according to Mehlich (83). Soil moisture was measured gravimetrically and pH was quantified using a PHS-3C pH meter (Shanghai, China) with 1:2.5 vol soil:H_2O solutions (84). Soil carbon (C) concentration was obtained by dividing OM by the van Bemmelen factor 1.72. In addition, three stoichiometric ratios were computed, i.e. the C:N, N:P and C:P ratios. Finally, mean annual temperature (MAT) for each site was obtained from CHELSA (79).

Outliers were tested by identifying values outside mean±SD, leading to 3 outliers for OM, 6 for AP, 4 for NO_3^- and 2 for NH_4^+, which were replaced using geostatistical interpolation where the unknown value of a given variable at a location x_i was predicted using the values at surrounding locations (68).

Statistical analyses

The dissimilarities among bacterial communities were calculated as Bray-Curtis dissimilarities for each pair of samples based on the double square root-transformed relative abundances of OTUs (for taxonomic dissimilarity) and double square root-transformed abundances of the nine N-related functional groups (for functional dissimilarity). By transforming the data prior to calculating dissimilarities, more weight is given to OTUs and functional groups with low abundance which would be overlooked otherwise. Double square root transformation was chosen based on preliminary analyses (e.g. having the highest model performance, see below) and favoured over logarithmic transformation because it avoids the troubles of transforming

zeros and resulting negative numbers. Nevertheless, the dissimilarity values do not drastically change depending on the transformation (Fig. S3-S4). As the geographic coordinates existed only for the centers of each site (consisting of 5 plots located 20 m from the center of the site), we randomly added or subtracted 20 meters from y- and/or x-coordinates of the sites to obtain unique coordinates for all plots and reflect the non-zero distances among the plots of a same site.

General relationships among taxonomic, functional and environmental dissimilarities and geographic distances among the plots were assessed by Mantel tests. For Mantel test, environmental dissimilarity was calculated using Bray-Curtis statistic and log-transformed soil variables (except pH already on log-scale).

To assess in detail the influence of individual environmental variables and distance on taxonomic and functional dissimilarities, we implemented generalized dissimilarity modelling, (GDM; 85, 86). GDM is suited to analyse spatial patterns of pairwise dissimilarities for community data as a function of environmental conditions and/or geographic distance (see e.g. in 87). Non-linear responses are possible by applying link and variance functions, and I-splines (see 85). Using GDM, we assessed (1) to what extent each environmental predictor and geographic distance alone explain taxonomic and functional dissimilarities, (2) what are the best combinations of predictors to explain taxonomic and functional dissimilarities, (3) how the predictors of the best models influence taxonomic and functional dissimilarities (i.e. shape of the relationship between a predictor and taxonomic or functional dissimilarity across the range of predictor values), and (4) how the importances of environmental predictors and distance vary across spatial scales.

For the GDMs, we created all possible combinations of environmental variables and distance but removed the combinations that contained correlated environmental variables (using threshold of ±0.7; see Table S2). No transformations were applied to environmental variables and distance, as GDM can model non-linear responses. This means that the results of the GDMs did not depend on the transformations applied to variables when analysing the relationships between dissimilarities/distance. Models for taxonomic dissimilarity (based on the 96 plots for which taxonomic composition was available) and functional dissimilarity (based on the same 96 plots or all 195 plots) were then built using the different combinations of predictors, and for each combination, the model deviance explained (%) was calculated. The best combination of predictor variables was determined as the model with the highest deviance explained and where all predictors were significant. Significance and contribution of predictors in the models were tested using permutation tests randomizing each predictor at a time, and testing the significance and amount of decrease in deviance explained compared to the model with unshuffled predictors (see function gdm.varImp; 86).

To examine the relationships between predictors and taxonomic and functional dissimilarities, we plotted the I-splines (i.e. response curves) fitted to the predictors retained for the best models. The height and slope of the curve indicate the amount and rate of change of community dissimilarity, respectively, along the predictor gradient. All models were fitted with three I-splines for all predictors with default knots (86).

Finally, to assess the scale dependency of these relationships and of the importance of environmental filtering and dispersal on taxonomic and functional dissimilarities, we divided all pairs of 96 plots into three equal sized groups based on the geographic distances among the

plots (i.e. three groups corresponding to short, medium and long distances between plots, namely 20 m to 314.3 km, 314.3 to 671.3 km and 671.3 to 1,545.6 km, respectively). For each group, correlation tests were run and the GDM modelling of taxonomic and functional dissimilarity was repeated.

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Figures

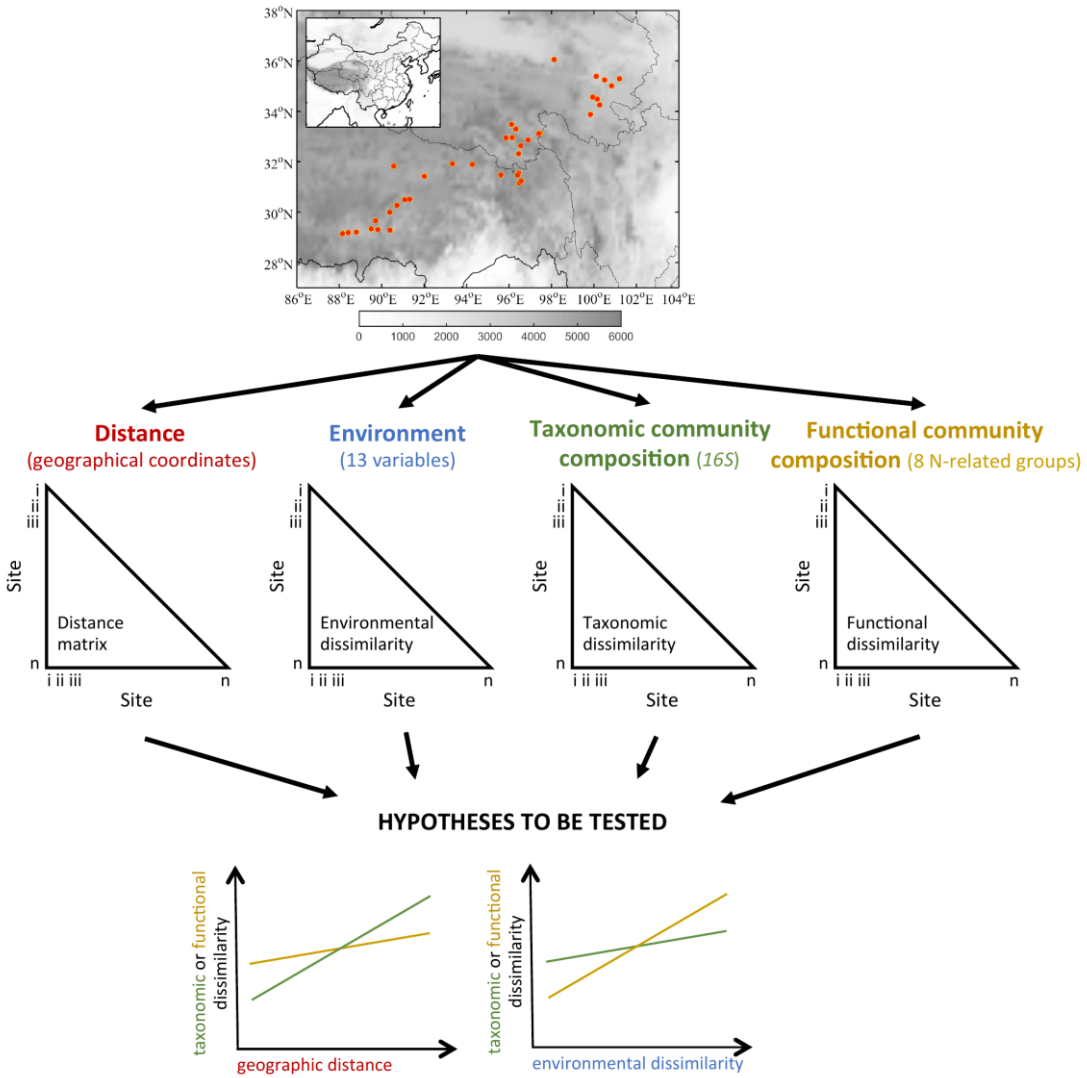
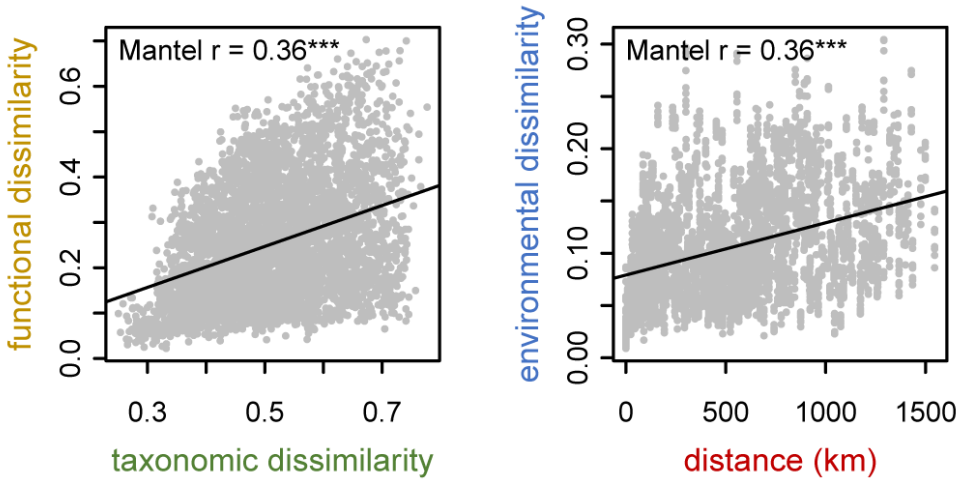


Figure 1. Framework used to study the drivers of taxonomic and functional biogeography of soil bacteria, and working hypotheses. Soil was sampled from 39 sites (red dots - 5 plots per site) along a 1,550 km transect in the Tibet plateau (Top). Distances, and environmental, taxonomic and functional dissimilarities among all plots were then computed and compared (Middle). We hypothesised that geographic distance would better explain taxonomic dissimilarity of bacterial communities due to dispersal processes, whereas functional rather than taxonomic dissimilarity would be mainly driven by environmental dissimilarity due to functional redundancy (Bottom).



694

695 **Figure 2.** Relationships between (Left) the functional and taxonomic community dissimilarities
696 and (Right) the environmental dissimilarity and geographic distance, based on the 96 soil
697 samples for which both taxonomic and functional compositions are available. Spearman
698 correlations (panel corners) are based on Mantel tests. Lines indicate linear fits.

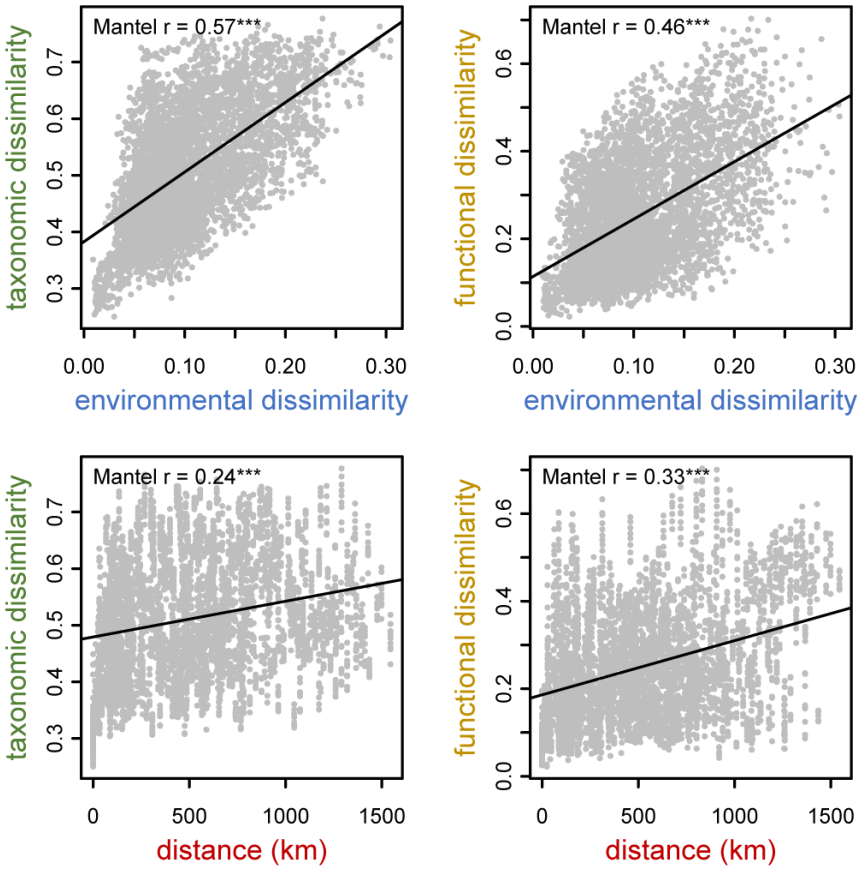


Figure 3. Relationships between the taxonomic (Left) or functional community dissimilarity (Right) and geographic distance (Top) or environmental dissimilarity (Bottom) based on the 96 soil samples for which both functional and taxonomic compositions were available. For 195 sites, see Fig S7. Spearman correlations (panel corners) are based on Mantel tests. Lines indicate linear fits.

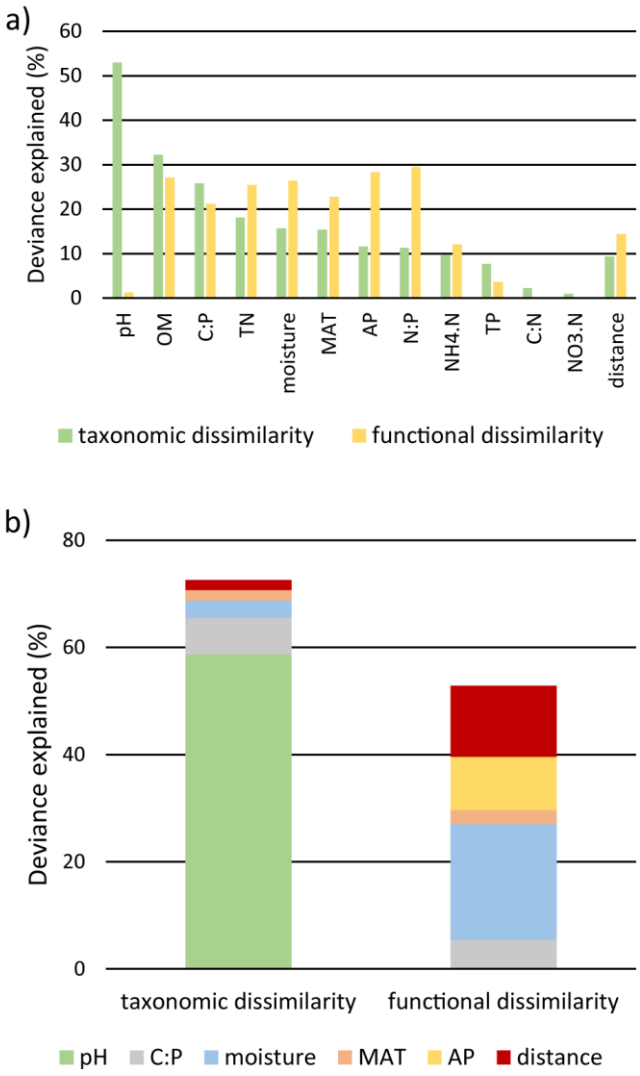
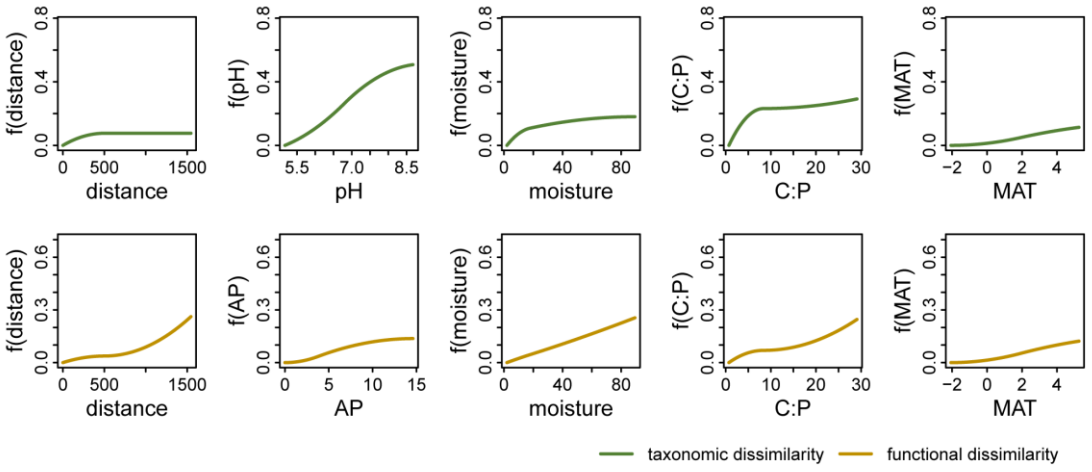
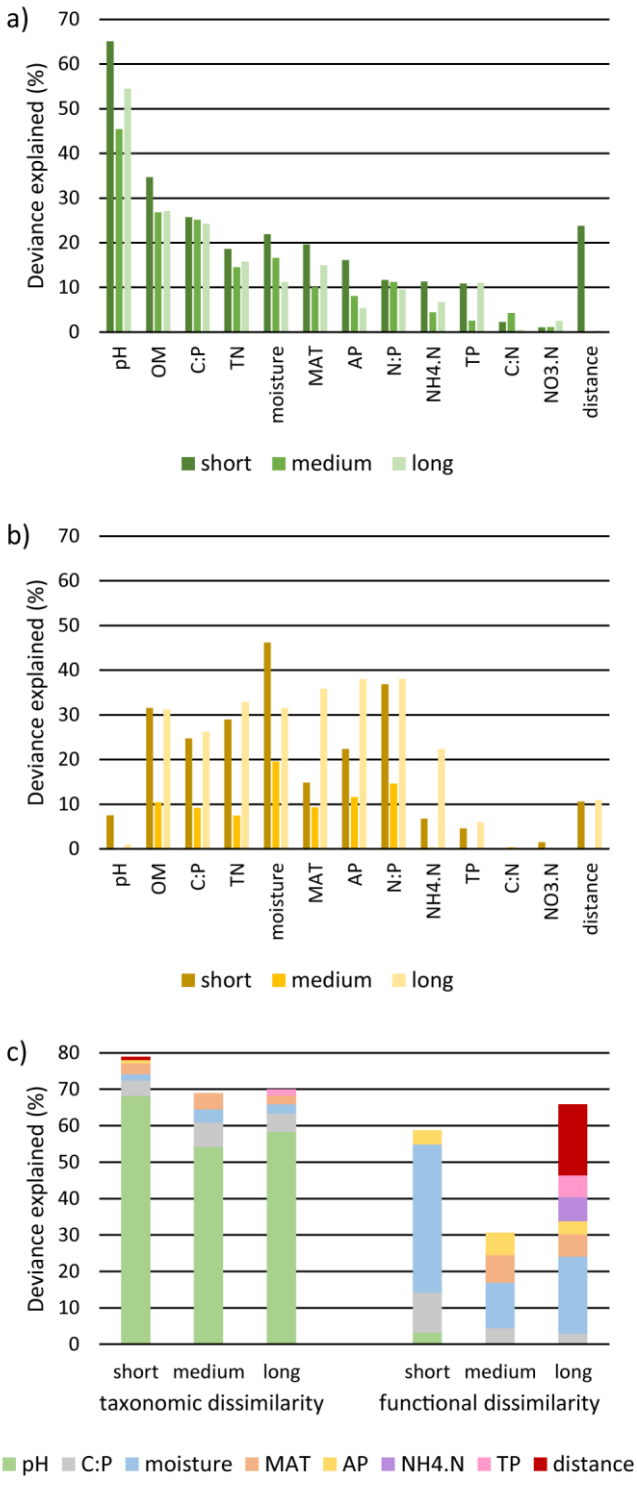


Figure 4. Percentage of deviance of taxonomic (a) and functional (b) dissimilarity explained by individual predictors, i.e. distance or each of the environmental variables; and the models with highest deviance explained when all predictors are significant and the relative importances of the predictors (c). Analyses were made based on the 96 soil samples for which both functional and taxonomic compositions were available. For results based on the 195 sites, see Fig S8.



712

713 **Figure 5.** Predicted changes in (Top) taxonomic and (Bottom) functional dissimilarity according
714 to changes in distance or each individual environmental variable selected by the best GDM
715 models (see Fig. 4), along the range of variable values. The maximum height and slope of the
716 curve indicate the amount and rate of change of community dissimilarity, respectively. The
717 analyses were made based on the 96 soil samples for which both functional and taxonomic
718 compositions were available. For 195 sites, see Fig S9.



719

720 **Figure 6.** Percentage of deviance of taxonomic (a) and functional dissimilarity (b) explained by
721 individual predictors when distinguishing three classes of distance between plots: 20 m to 314
722 km, 314 to 671 km, and 671 to 1,546 km (in dark, intermediate and light, respectively), and the
723 models with highest deviance explained when all predictors are significant and the relative
724 importances of the predictors (c). For each model considered, all predictors were significant.